Stress Effects on Natural Ecosystems
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CHAPTER 8

Influence of Environmental Stressors upon Energy Flow in a Natural Terrestrial Ecosystem

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INTRODUCTION

Stress is a physiological state of a biological system resulting from its response to environmental stressors. Stressors are any situation, condition, quality, or intensity of environmental factors which cause a biological system to mobilize its resources and increase its expenditure of energy.

These definitions are compatible with those of Selye (1956) and Fitch & Johnson (1977) and support the conclusion of H.T. Odum (1967) that, although different stressors have different impacts on organisms or ecosystems, all impacts divert potential energy flows that otherwise could perform useful work in the system. If, then, stress involves a drain or diversion of calories of potential energy, it should be possible to obtain a quantitative measure of ecological stress by monitoring changes in energy flows, loss of specific pathways, or the acceleration of repair processes. Lugo (1978) reviewed the literature dealing with ecosystems and stress and suggested that ecosystem complexity is a function of the balance between energies that contribute to growth and organization and those that contribute to disorder. Disorder in this context is the disruption of

ecosystem structures or functions. Energy required for ecosystem recovery and maintenance contributes to order in the system.

A common measure of energy production in ecosystems is primary productivity. It, like most ecosystem properties, responds differently to different stressors, e.g., productivity may be little affected by fire or harvest, while drought usually has devastating effects.

Our objectives are to describe the influence of environmental stressors upon natural ecosystems in terms of quantitative changes in energy processes, such as primary productivity. As the biological components of ecosystems are normally species populations, our analysis includes responses of individual populations as well as whole-system properties. To fulfil these objectives it is necessary to quantify the intensity of environmental stressors, as well as to follow changes in energy pathways within the ecosystem. We do this on temporal and spatial scales because there are pronounced variations in environmental stressors—both seasonally and from one habitat to another. A specific objective is to develop a flow-diagram—an energy model—of 'island' ecosystems which identifies the sources and magnitudes of energy required to compensate for disorder created by environmental stressors.

Experimental Ecosystems

Terrestrial ecosystems which occur in depressions on granite outcroppings along the fall-line of the southeastern United States have often been used to investigate the ecological effects of a variety of natural and anthropogenic stressors (McCormick & Platt, 1962; Cumming, 1969; Lugo, 1969; Murphy & McCormick, 1971; Mellinger, 1972; Meyer *et al.*, 1975; Shure & Ragsdale, 1977). These small, natural, yet manipulable, ecosystems resemble 'islands' scattered on a sea of granite (Fig. 8.1). Attributes which cause these 'island' ecosystems to be so well suited for experimental ecosystem studies are reviewed by Platt & McCormick (1964) and by McCormick *et al.* (1974). Among these characteristics are their relatively small size, well-defined boundaries, few species but high population densities, well-defined zonation of species, both annual and perennial floras, an extraordinarily high degree of endemism, and associated adaptations to a high-stress environment.

A particularly unusual characteristic of these manipulable terrestrial ecosystems is the one-to-one correspondence between the temporal sequence of occurrence of species during primary succession and the spatial sequence of occurrence of species in discrete zones, or habitats, from the periphery to the centre of the ecosystem. The reason for this unusual correspondence between temporal and spatial occurrence of species is the dominating influence of substrate availability and quality. Soil depth and

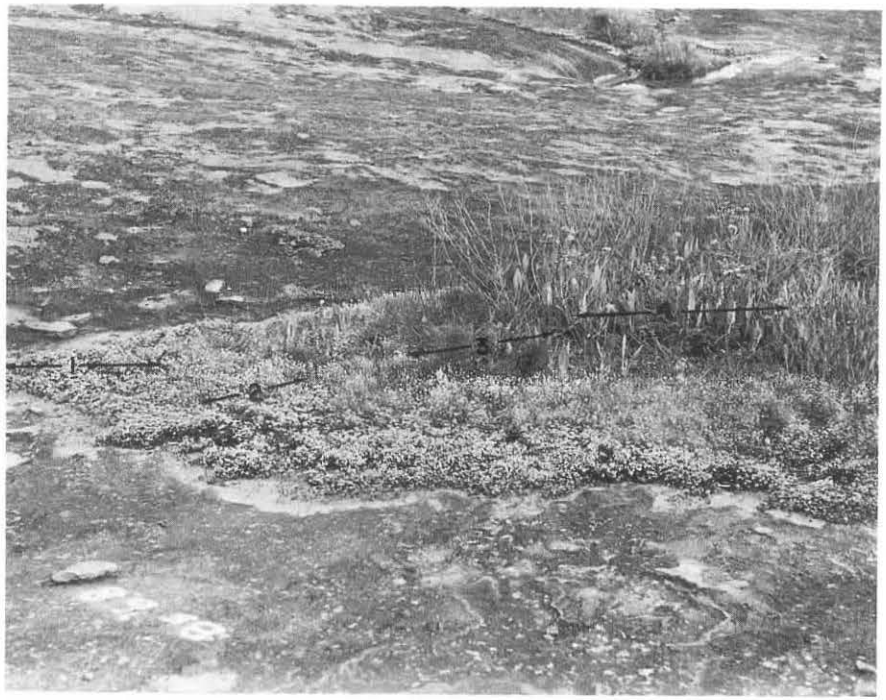


Fig. 8.1 An 'island' ecosystem on a granite outcrop near Atlanta, Georgia, USA. Note the zonation, marked by species, into distinct habitats which correspond to successional series: (1) *Sedum smallii*, (2) *Minuartia* sp., (3) *Viguiera porteri*, and (4) *Senecio tomentosus*. Its height of 20 cm indicates the scale.

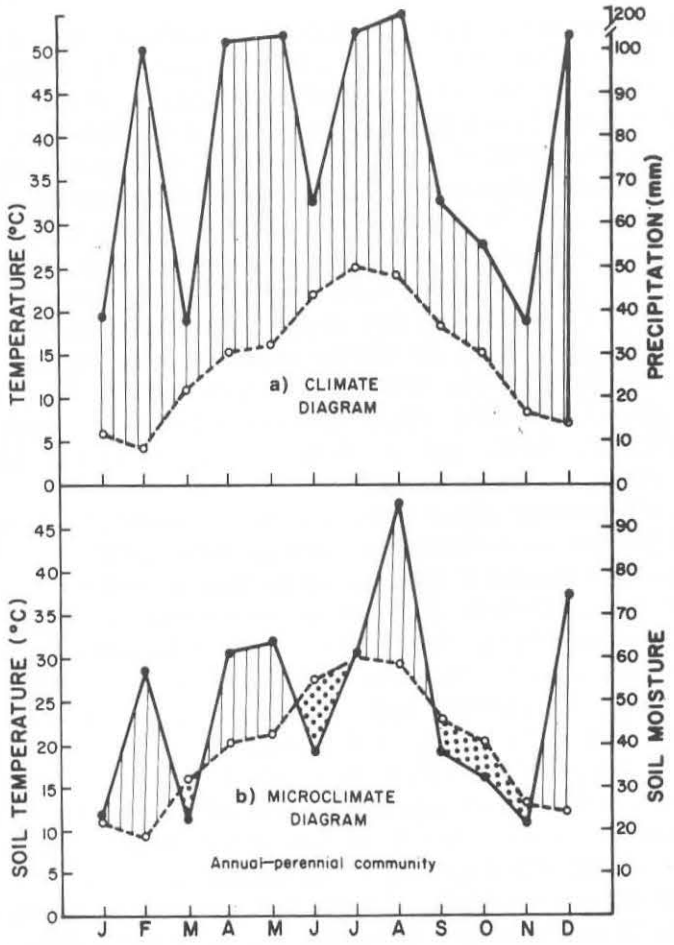
associated moisture availability increase gradually and continually along both temporal and spatial gradients in these 'island' ecosystems. Primary succession proceeds at a rate and in a direction dictated by the accumulation and development of soil in small bowl-shaped depressions on the rock surface. Soil depth and moisture also increase from the periphery towards the centre of these 'island' ecosystems and successional species occur in distinct zones corresponding to the resulting intensity gradients.

These zones are identified by either the dominant species or the successional stage which is or are represented in each zone. Only lichens and occasional mosses colonize exposed rock surfaces. When soil has begun to accumulate in depressions, the outer zone of minimal depth of soil is dominated by a pioneer species, *Sedum smallii*. As soil accumulates to a depth of 4 cm or more, species of *Minuartia* and scattered colonies of the moss genus *Polytrichum* become established. When the soil reaches a depth of 10–12 cm, a variety of species, dominated by *Viguiera porteri*,

constitute an annual herbaceous community (Burbanck & Platt, 1964). The next stage in the sere, occupying deeper soils in the adjacent interior zone, is an annual–perennial community in which *Senecio tomentosus* is usually the dominant species.

The Environment — Stress and Stressors

While the climate of the region is extremely favourable for plant growth and high productivity (Fig. 8.2a), the microclimate of these 'island' ecosystems near Atlanta, Georgia, provides severe stress conditions which approach the limits of tolerance of most plant and animal species (Fig. 8.2b to d). Differences between the climate of the region and the



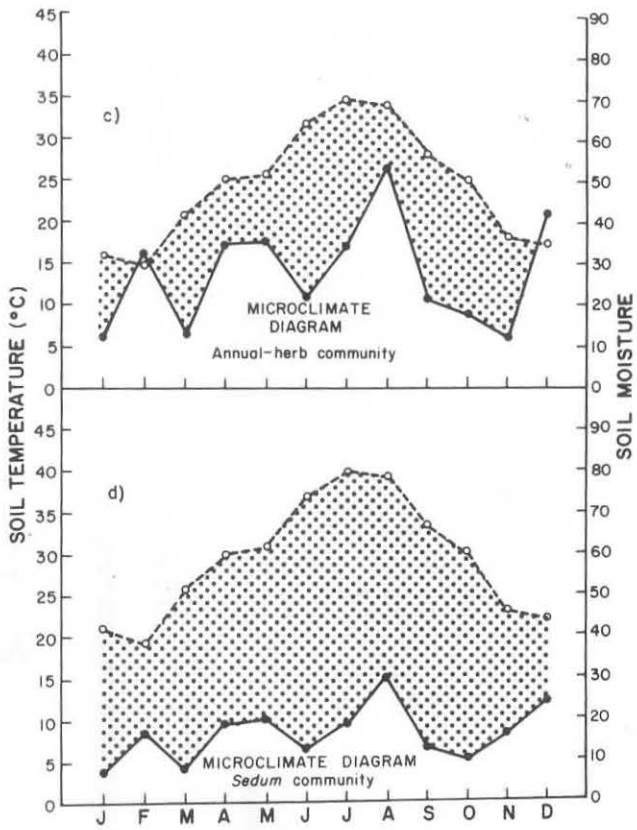


Fig. 8.2 a) Climate diagram for Chapel Hill, North Carolina, where most of this study was conducted on simulated granite outcrops (Platt & McCormick, 1964). The climate diagram is constructed according to the techniques of Walter & Lieth (1960). Vertical lines represent climatic conditions favourable for plant growth. The dotted pattern, used in the microclimate diagrams when the moisture curve drops below the temperature curve, represents conditions unfavourable for plant growth. b–d) Microclimate diagrams of successive zones or habitats beginning in the centre of the 'island' ecosystems. Because these habitats are also successional sequences (seres), Fig. 8.2 represents long-term variations in microenvironment, as well as annual and spatial microenvironmental fluctuations. Transformation of climate diagrams to microclimate diagrams involves using soil temperature of specific habitats or seres instead of air temperature, and using the percentage of soil moisture instead of precipitation. In order to maintain the appropriate-scaled relationship between temperature and precipitation, soil-moisture data were converted to the precipitation required to produce a specific soil-moisture condition. Therefore, the right-hand ordinate is a scaled representation of soil moisture, not a direct measure of the percentage of soil moisture. Soil temperature and other data are derived from several sources, including Cumming (1969), Mellinger (1972), and Shure & Ragsdale (1977).

microclimate of specific habitats within these ecosystems is due primarily to the geomorphology of the granite outcrops.

Lugo (1978) reviewed properties of physically controlled biologically accommodated and stressed ecosystems, finding that these 'island' ecosystems are excellent examples of physically controlled and highly stressed ecosystems. Major stressors are the limited substrate and nutrient availability, limited moisture availability, and extreme and rapidly fluctuating temperatures. Fluctuations vary in intensity and magnitude along spatial and temporal scales. Temporal fluctuations are both diurnal and seasonal. Figure 8.2 illustrates temporal fluctuations in microclimate in specific habitats within the 'island' ecosystems. Figure 8.3 illustrates an

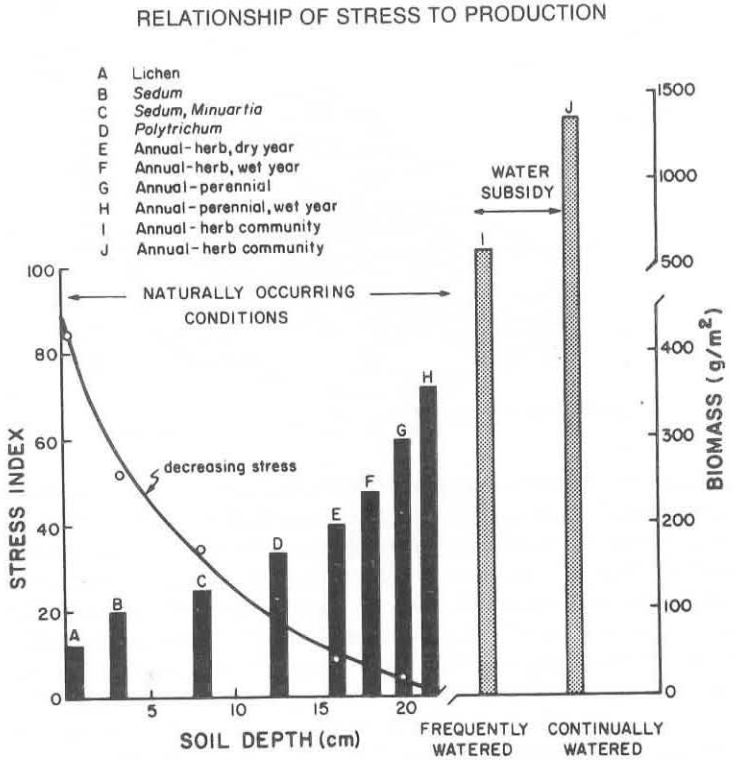


Fig. 8.3 The stress index is the mean of summed values of three stressors: temperature, water, and nutrients. For each stressor the range and optima of conditions or intensities were determined. Optima were based upon responses of populations of dominant species of each habitat or sere. Stress is expressed as the percentage of deviation from optimal conditions experienced in the field. Data used to derive the stress index come from McCormick & Platt (1962), Cumming (1969), McCormick *et al.* (1974), and Meyer *et al.* (1975).

inverse relationship between the intensity of major environmental stressors and net primary production. This figure also illustrates the direct correspondence between increasing soil depth and the temporal and spatial occurrence of species and species associations.

The severity of environmental stressors varies inversely with the above. Structural and functional adaptations of individual species and whole ecosystem properties to this extremely high-stress environment cause these particular ecosystems to be well suited for studies of stress ecology. The highly endemic flora of these 'island' ecosystems occupies an ecological niche that is uninhabitable by the flora and fauna that is characteristic of the region (McCormick *et al.*, 1971).

Population Responses to Environmental Stressors

Plants that occur in relatively deep soils where moisture stress is less severe than in surrounding areas, where soil-temperature fluctuations are less extreme, and where the pool of available nutrients is not severely limiting, exhibited 'normal' gas-exchange patterns (Fig. 8.4a). However, those that normally occur in shallow soils under extreme conditions exhibited gas-exchange patterns with pulses of activity during those periods when conditions of stress were reduced. Low-stress periods were night-time, early morning, and evening. Under extreme conditions, the pattern of gas exchange was typical of plants with CAM metabolic pathways (Burris & Black, 1976). These findings and details of experimental procedure are described by Lugo (1969). Results are consistent with reported metabolic behaviour of plants in other stressed ecosystems, such as those of the sub-alpine region (Tranquilline, 1963), sand dunes (Willis & Jefferies, 1963), deserts (Walter, 1963), and in arctic and alpine regions (Billings & Mooney, 1968).

In general, outcrop plants show one of two strategies of survival to temporal patterns of environmental change. One group of non-vascular plants and a few vascular perennials exhibit slow rates of growth over long periods of time. Metabolic activities in these plants are reduced as soil moisture becomes limiting; they withstand desiccation and growth is slowly resumed when moisture conditions become favourable. Examples of this group include *Polytrichum* spp., *Selaginella rupestris*, and *Senecio tomentosus*. The other group is composed of annual vascular plants. Members of this group exhibit explosive growth rates when moisture conditions are favourable but are capable of withstanding conditions of stress for short periods of time. Examples of this group include *Viguiera porteri*, *Hypericum gentianoides*, and *Crotonopsis elliptica*.

Different growth strategies of these two groups are reflected in the magnitudes of photosynthetic (P) rates. Species which exhibit explosive growth rates are capable of high photosynthetic rates at high light

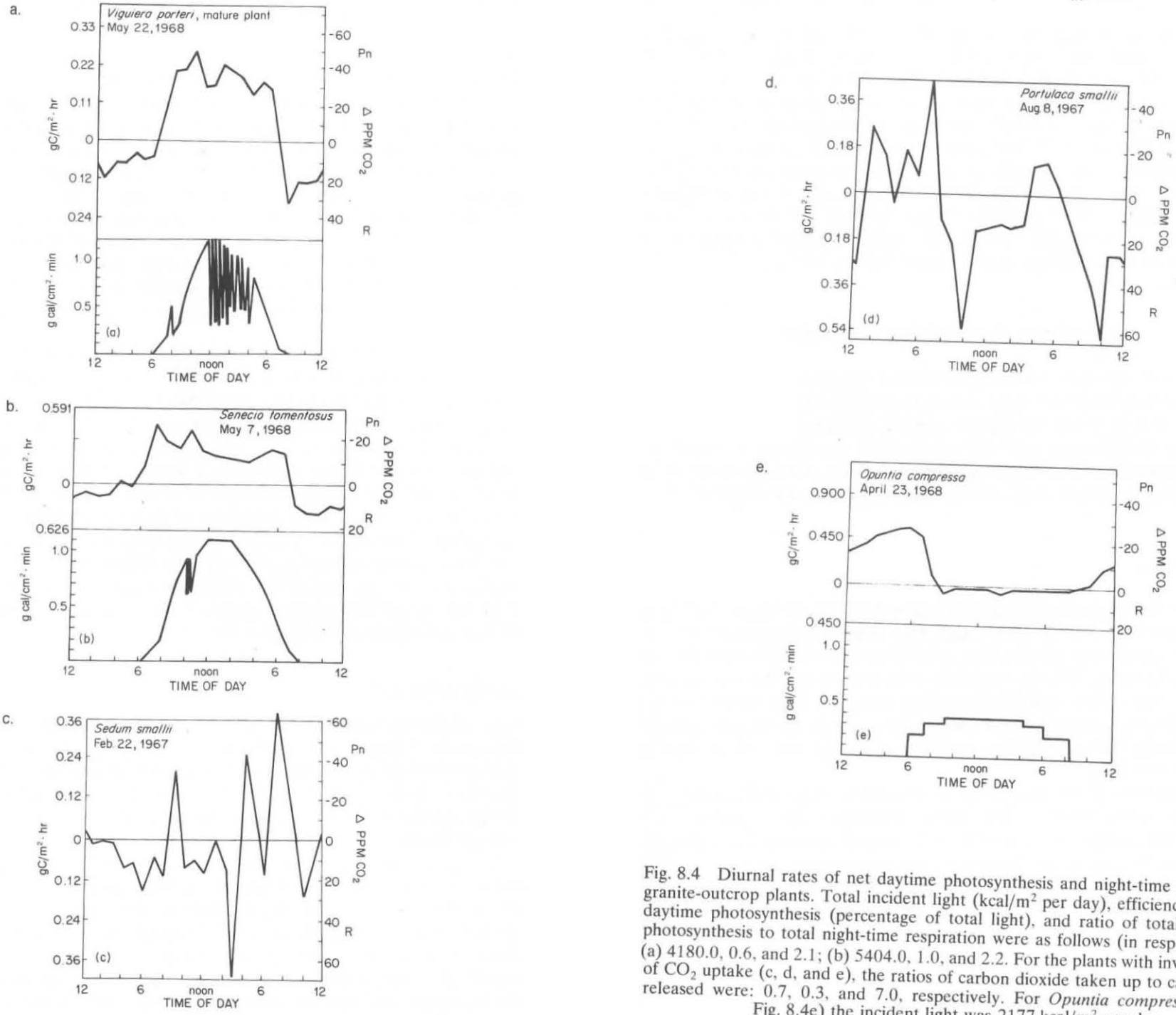


Fig. 8.4 Diurnal rates of net daytime photosynthesis and night-time respiration of granite-outcrop plants. Total incident light (kcal/m^2 per day), efficiency of total net daytime photosynthesis (percentage of total light), and ratio of total daytime net photosynthesis to total night-time respiration were as follows (in respective order): (a) 4180.0, 0.6, and 2.1; (b) 5404.0, 1.0, and 2.2. For the plants with inverse patterns of CO_2 uptake (c, d, and e), the ratios of carbon dioxide taken up to carbon dioxide released were: 0.7, 0.3, and 7.0, respectively. For *Opuntia compressa* (above in Fig. 8.4e) the incident light was 2177 kcal/m^2 per day.

intensities. Sustained high photosynthetic rates during the day, high *P/R* ratios during sunny days, and low *P/R* ratios during cloudy days are indicators of adaptations to high light conditions. Earlier we reported that these species are also characterized by low chlorophyll **a** content, high Margalef pigment ratios, and high caloric value (McCormick *et al.*, 1974).

The group of plants with slow growth rates exhibits a wider variety of metabolic patterns. For example, *Senecio* at times exhibited high photosynthetic rates (Fig. 8.4b) but during cold weather reduced its metabolism significantly (Lugo, 1969). Patterns of gas exchange for succulent species (Fig. 8.4c, d, e) were equally variable. We earlier reported a lower caloric value for the tissues of this group (McCormick *et al.*, 1974).

Ecosystem Responses to Stressors

Responses at the ecosystem level depend upon the collective adaptations of individual species. However, there are characteristics that are unique to the system *per se* (e.g. total chlorophyll content, leaf-area indices, diversity, and biomass distribution) and that also reflect conditions to which the system is responding. Results of chlorophyll studies were discussed in an earlier paper (McCormick *et al.*, 1974); other attributes are discussed next.

Leaf Area Index

The ratio of leaf area to ground area covered (LAI) has been correlated both with rainfall (Walter, 1963) and with plant productivity (Wassink, 1968). Ecosystems that receive low rainfall usually exhibit low LAI and low net productivity. This is consistent with our results. Granite outcrop communities have a low annual productivity and a low LAI of from 1 to 2. Similar LAI values were reported for granite outcrops by Murphy (1970). However, during the short summer growing season in this system, rates of productivity were high.

The architecture of the canopy is an important factor influencing light interception. Annual-herb communities dominated by *Viguiera* form horizontal leaf canopies with a LAI of 2. Annual–perennial communities dominated by *Senecio* have similar LAI values but intercept less radiation as a result of their vertically oriented leaves. The *Viguiera* morphology is favourable for rapid growth but is prone to overheating. The *Senecio* morphology is favourable to slower growth but is more efficient for protection from intense solar radiation. Both occur in the granite outcrop landscape and are adaptive, as *Viguiera* is an annual adapted to fast growth, while *Senecio* is a perennial that grows at a slower rate.

Biomass

Biomass content of a system is the net result of the rate of primary productivity *minus* energy used in maintenance. Above we advanced the hypothesis that, with increasing intensity of environmental stressors, the amount of biomass that a system can sustain should decrease. Figure 8.3 substantiates this hypothesis. Along a spatial gradient of environmental stressors, we observed a logarithmic decrease in ecosystem biomass ($r^2 = 0.96$), which we attribute to increased cost of maintenance associated with drought, diminished availability of nutrients, and excessive heat.

Dynamics of biomass accumulation may partially be understood by elucidating the temporal pattern of primary productivity by the system. This response pattern for each habitat, or successional stage, is shown in Fig.8.5.

In granite-outcrop ecosystems the annual net primary production is low, and the growth season is limited to about 100 days for each of its two distinct annual floras (Mellinger, 1972). Most of the biomass of this system is in the form of dead matter—especially standing dead matter, as opposed to litter. This feature lowers the maintenance cost during periods of intensive stress and also represents a storage of nutrients that are tightly bound to the system. Accumulation of standing dead organic matter has adaptive value in its high retention of mineral nutrients in the 'island' ecosystem. Observed heavy runoff during rains, sandy soils (Nesom, 1969), and low available mineral content in soils (Meyer *et al.*, 1975) confirm the significance of this adaptation. Minerals stored in dead matter become available during the summer season when respiration rates in soils are highest and moisture is available (Fig. 8.6).

Species Diversity

Some of the best available data on the diversity of different species come from the studies of Shure & Ragsdale (1977), but our less-detailed and independent studies lead to the same conclusions as were reached by those authors. Species diversity of plants, microarthropods, and macroarthropods increases during succession. Density and biomass of plants and macroarthropods also increase during succession.

The quantitative index of stress illustrated in Fig. 8.3 represents both temporal (successional) and spatial (habitat) gradients of environmental stress. Thus, as the intensity of stressors increases, either temporally or spatially, plant and animal diversity decreases. Maximum Shannon–Weiner diversity values are approximately 1.4 for plants and 2.3 for soil arthropods. Diversity indices are low when compared with those reported in the literature for systems without stress, but are in the same order of

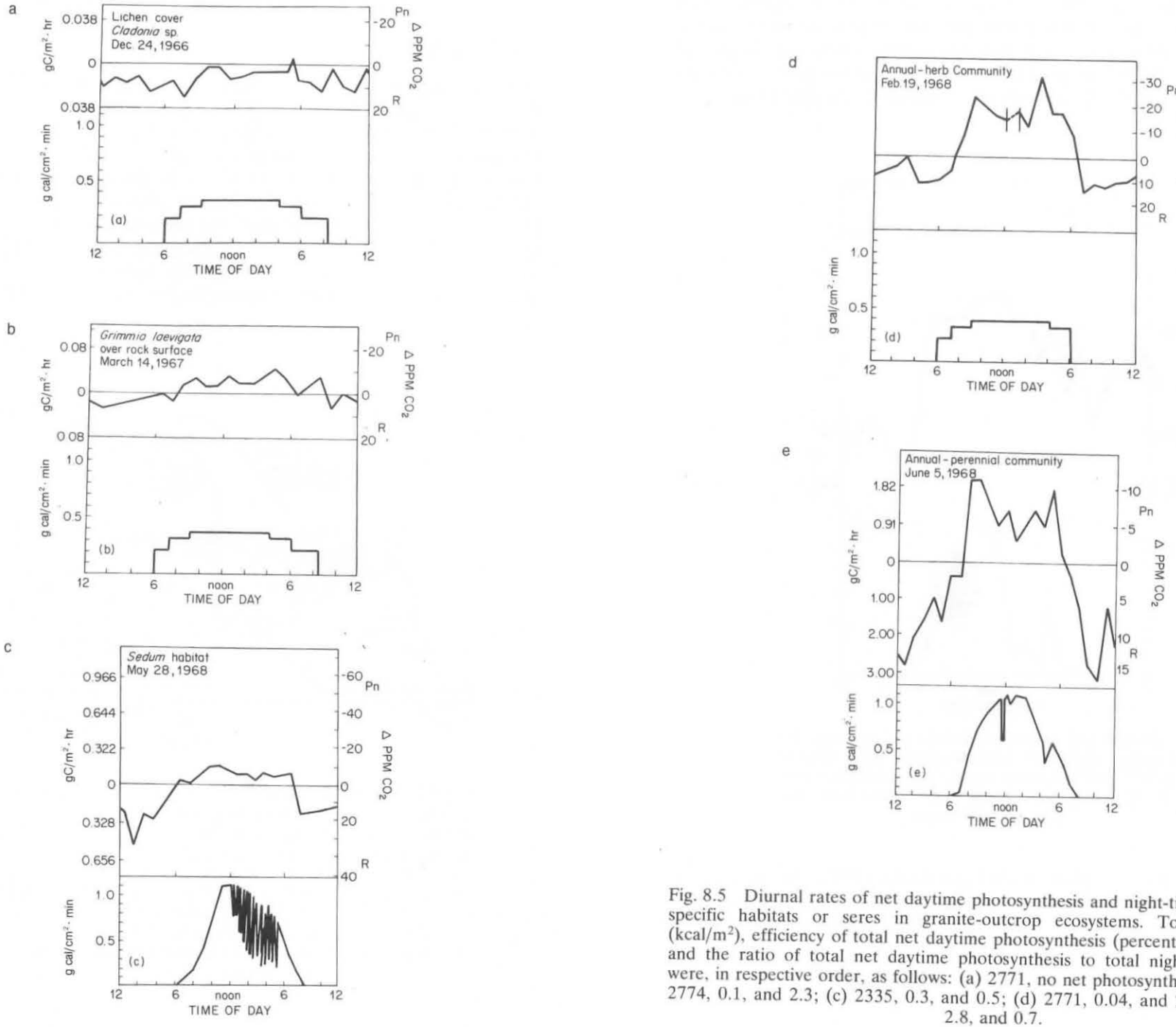


Fig. 8.5 Diurnal rates of net daytime photosynthesis and night-time respiration for specific habitats or seres in granite-outcrop ecosystems. Total incident light (kcal/m^2), efficiency of total net daytime photosynthesis (percentage of total light), and the ratio of total net daytime photosynthesis to total night-time respiration were, in respective order, as follows: (a) 2771, no net photosynthesis measured; (b) 2774, 0.1, and 2.3; (c) 2335, 0.3, and 0.5; (d) 2771, 0.04, and 2.0; and (e) 5100, 2.8, and 0.7.

magnitude as those reported for stressed systems (E. P. Odum, 1971; Krebs, 1972). Plant diversity and overall evenness tend to be highest at the peak of the growing season, when potential energy sources are high, and decrease with the onset of winter stress. Early in the growing season (April), evenness is low, owing to the explosive germination of *Viguiera* seeds.

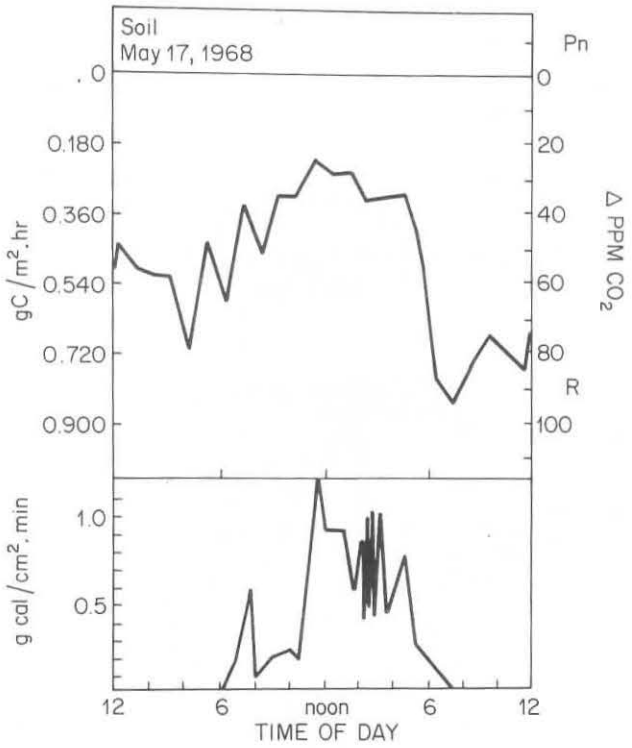


Fig. 8.6 Diurnal rate of carbon dioxide gas exchange for the soil surface devoid of vascular plants. Total incident light was 3871 kcal/m^2, there was no detectable photosynthesis in the bare soil, and total respiration was 11.7 gC/m^2 for 24 hours.

In the studies of E. P. Odum (1971) and Krebs (1972) the diversity of macro- and microarthropods was unexpectedly high in pioneer (high-stress) stages, especially in the autumn (fall) season. This could be attributed to a seasonal food pulse in the form of maximum seed storage and the beginning of germination in these zones (Sharitz & McCormick, 1973).

Primary Productivity and Respiration

Carbon Budget

Figure 8.7 depicts the carbon budget of the ecosystem on a favourable day during the summer growing season. Highest carbon storages are in the form of dead organic matter, especially in the soil. Night-time ecosystem respiration was 16.3 gC/m^2 but is doubled to estimate 24-hour respiration. Soil respiration accounted for 8.0 gC/m^2 in the day and plant respiration for 12.4 gC/m^2 in the night. As daytime photosynthesis was 14.3 gC/m^2, plants respired 86 per cent of their net primary productivity and their *P/R* ratio was 1.1. The ratio of photosynthesis to total ecosystem respiration was lower than 1 due to soil respiration. However, soil respiration was dependent mostly on energy storages in the form of litter from the previous year's growth.

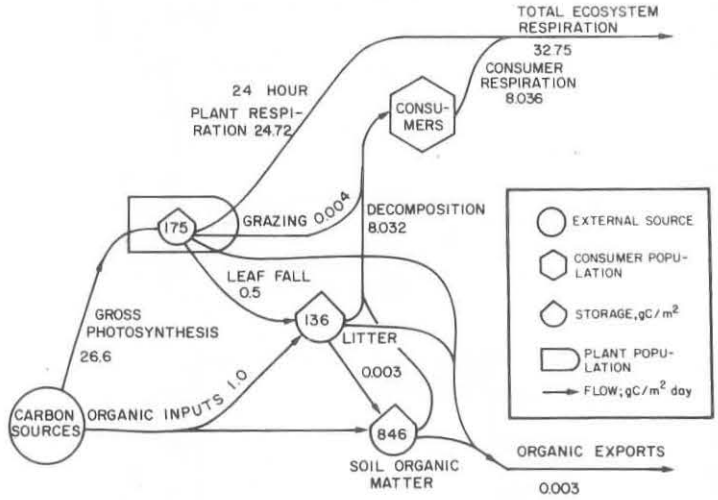


Fig. 8.7 The carbon budget for a herbaceous annual–perennial granite-outcrop ecosystem during a day in June. Numbers inside the storage symbols represent the carbon content of the compartments in gC/m^2. Lines represent the flow of carbon between compartments and the numbers above or below the lines represent the rate of carbon flow in gC/m^2 per day. Arrows indicate the direction of flow. The diagram is based on data obtained using natural ecosystems transplanted to simulated outcrop substrata in the North Carolina Botanical Garden. Symbols are after H. T. Odum (1971).

Lemon (1963) reported that, during the night period, the respiration of a cornfield was 25 per cent of the daily net production. For an old-field, Golley (1960) reported a magnitude of 56 per cent for the same parameter. The granite outcrop, with respiration of 86 per cent of the net primary productivity of its plants, seems to be at the other extreme of the range from the cornfield. These values are indicative of the effects of environmental stressors. Heat and moisture stress in granite-outcrop habitats cause greater energy loss through plant respiration than in old-fields (where more mesic conditions occur) or in cornfields (where Man actively reduces some of the stress). However, since daytime respiration is not known, differences among systems could be larger or smaller than are indicated by night-time respiration rates.

Cumming (1969) demonstrated that the soil moisture was above the wilting point for only 100 days during the 1967 growing season. Using data from the carbon budget, we can calculate the excess of daytime organic production by subtracting plant respiration from daytime photosynthesis. The value obtained is 1.94 gC/m^2 or 3.88 g of organic matter per m^2 per day (using 2 as a factor to convert carbon to organic matter). Assuming this production for 100 days, we obtain a yield of 388 g of organic matter per m^2 per growing season. A harvest on 28 August yielded 354 g/m^2 (Table I). Thus, the carbon dioxide analyser method for measuring productivity and the carbon budget calculations were consistent with observed field growth.

Related to the carbon budget is the accumulation of organic matter in 'island' ecosystems. Organic matter accumulates from three sources: plant productivity, import from other 'islands', and dust. The present rate of accumulation of organic matter for an annual–perennial community was calculated from the organic content in the soil (Table II) and an age estimate of 679 years (Burbanck & Platt, 1964). The calculated rate of 1.26 gC/m^2 per year suggests that these 'islands' are in near-steady-state

Table I Distribution of biomass in an annual–perennial community at the North Carolina Botanical Garden on 28 August 1967.

Plant component	Dry weight, g/m^2	Percentage of total
Leaves	95	26.8
Stems	161	45.5
Inflorescences	8	2.3
Attached dead matter and miscellaneous species	42	11.9
Total biomass above ground	306	86.5
Roots	48	13.5
Total biomass	354	100.0

Table II pH and organic matter content of selected outcrop soils.

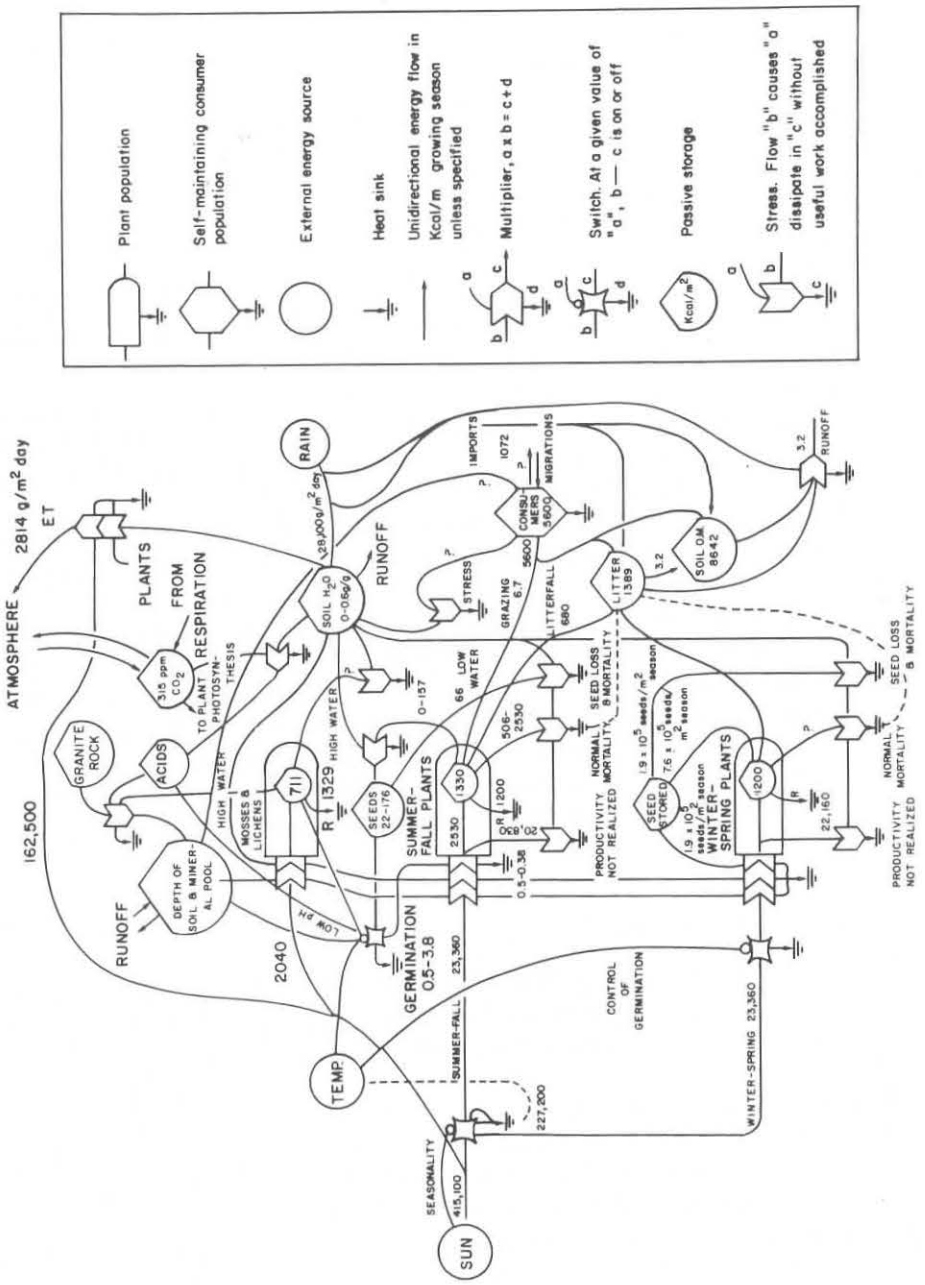
Location	Source of soil sere or habitat	pH	Organic matter, %
N.C. Botanical Garden	Annual–perennial	5.7	2.68
N.C. Botanical Garden	Annual-herb community	4.4	2.14
Mt Arabia	Annual–perennial community	4.3	3.25
Mt Arabia	Annual-herb community	4.2	2.29
Mt Arabia	*Polytrichum* mat	4.3	3.07
Mt Arabia	Under decomposing pine needles	4.1	24.36

conditions in relation to accumulation of soil organic matter. Thus, inputs of organic matter to the soil should balance losses. The output of organic matter from the granite-outcrop ecosystems of Panola Mountain, Georgia, was 0.02 g/m^2 per day and correlated with rainfall (Bostick, 1968).

Soil respiration during the summer accounts for the greatest loss of carbon if we assume low winter soil respiration and low rates of organic matter losses. Soil respiration over the summer period was calculated to be 700 gC/m^2 (Fig. 8.5). Inputs to this compartment included a litter-fall input of 0.5 gC/m^2 per day (obtained by dividing the annual production by 365 days). Murphy (1970) measured litter-fall rates of 0.2–1.9 gC/m^2 per day in similar ecosystems during the period of July to October. The input from outside sources was calculated by dividing measured imports by 365. These flows, *plus* the amount of carbon stored in the litter, are enough to maintain a steady-state condition between inputs to the soil system and outputs to summer respiration (Figure 8.7).

Efficiency of Photosynthesis

During a period of active growth (Fig. 8.5e), the efficiency of daytime net photosynthesis was 2.8 per cent of the total radiation or 5.94 per cent of the visible radiation (assuming that visible was 47 per cent of total radiation). Values are high and reflect the high photosynthetic capacity of these plants during favourable periods. Over the growing season, the efficiency of photosynthesis was 0.36 per cent of total radiation (1490 $kcal/m^2$ stored divided by 415,100 $kcal/m^2$ received multiplied by 100) or 0.76 per cent of the visible radiation. This value is comparable with those reported by Bliss (1962) for arctic and alpine communities. Species of the arctic and alpine tundra are also capable of high efficiencies when conditions are favourable, but over long periods of time, when stressors are operative, efficiencies are in the range of those observed in the granite-outcrop ecosystems (Bliss, 1962).



A Model of Ecosystem Structure and Function

Figure 8.8 was constructed by utilizing all of the data available to us on granite-outcrop ecosystem structure, function, and energy flow. It depicts the most important compartments, energy sources, stressors, and energy-flow pathways that are believed to be operational in granite-outcrop ecosystems. Storages and flows are based on mean values. Storages are expressed in kilocalories per square metre and flows in kilocalories per square metre per growing season when the pathway is active (134 days for the summer–fall flora and 120 days for the winter–spring flora).

The model depicts three external energy sources acting upon the system: sunlight, temperature, and rain. Solar energy input into the winter–spring and summer–fall subsystems is similar, but each phase of the flora is subjected to different light, temperature, and rainfall régimes.

Seed budgets are presented in the model and are based on the work of Mellinger (1972) and Sharitz & McCormick (1973). Factors contributing to seed production and germination are rainfall, depth of soil, pH, moss and lichen cover, temperature, and water-level. Rainfall accelerates seed production during high water conditions and contributes to seed loss and mortality during runoff conditions. Moss and lichen cover influence the water content of the soil and stimulate the germination of summer–fall plants such as *Viguiera.* Acids produced by geologic weathering processes, and the combination of carbon dioxide with water, lower the pH and stimulate seed germination. Temperature is believed to be the factor that 'switches' on or off these and other germination prerequisites.

Two factors that regulate the photosynthetic process are water and nutrient availability in the soil; both are related to soil depth (McCormick *et al.*, 1974). However, the respiration of macroconsumers and soil microorganisms releases significant amounts of nutrients that may be immediately available to photosynthesizing plants. Organic imports into the system are higher than exports, suggesting that the system is very efficient in trapping and concentrating more organic matter than enters the system *via* runoff or dust. This efficiency accounts for the slow growth of these 'island' ecosystems.

The energy cost of stress was calculated by using our results together with the field observations of Cumming (1969), Mellinger (1972), and Sharitz & McCormick (1973). Of the total energy flux into the granite-outcrop ecosystem, about 40 per cent is utilized in water evaporation

Fig. 8.8 Energy diagram for a herbaceous annual–perennial granite-outcrop ecosystem. Numbers inside the storage symbols represent the accumulation of energy in the compartment in kcal/m² for the growing season. Arrows indicate the direction of flow. The model is discussed in the text. Symbols are after H. T. Odum (1971).

Table III Estimate of the rates of net daytime photosynthesis, night-time respiration, and water loss of granite-outcrop ecosystems based on soil and individual plant gas-exchange determinations. (Rates are representative of plant activity in the growing season.)

Ecosystem component	Photosynthetic area, m^2	Net daytime photosynthetic rate, gC/m^2 per day	Night-time respiration rate, gC/m^2 per day	Contribution to ecosystem metabolism, gC/m^2 per day		Mean rate of water loss, gH_2O/m^2 per day	Contribution to the water loss of the system, gH_2O/m^2 per day
				P	*R*		
Polytrichum commune	0.1	0.88	1.66	0.80	0.16	157	15
Grimmia laevigata	0.2	0.28	1.12	0.05	0.02	157*	31
Cladonia rangiferina	0.3	0.21	0.19	0.06	0.05	—	—
Viguiera porteri	1.0	7.28	1.04	7.28	1.04	1134	1134
Senecio tomentosus	1.0	5.90	2.62	5.90	2.62	938	938
Subtotal for plants	2.6			13.37	3.89		2118
Soil	—	—	8.91		8.91	696	696
Ecosystem totals	2.6			13.40	12.80		2814

*Rate not measured; assumed to be equal to rate in *Polytrichum commune*.

(Table III). During optimal conditions for plant photosynthesis, 6 per cent may be trapped by gross production (Fig. 8.7). Regardless of rainfall, conditions for maximum growth are limited by the water-holding capacity of the soil. We observed that, over the growing season, a percentage of the maximal productivity is not realized, owing to moisture stress. This value represents a normal energy cost of the granite-outcrop environment. We estimate this value to be 20,830 $kcal/m^2$ per growing season for each granite-outcrop seasonal flora (summer–fall and winter–spring). Of that productivity which is realized, there is an energy tax in the form of plant mortality prior to the completion of life-cycles. We estimate that this energy tax varies from 506 to 2530 $kcal/m^2$ per growing season. Variation in the energy tax depends upon rainfall. Energy drains for *Viguiera* seeds have been worked out by Mellinger (1972) and are also shown in Fig. 8.8. Loss of consumers was discussed by Bostick (1968), but was not quantified and cannot be estimated at this time.

These calculations demonstrate the high energy cost of the granite-outcrop environment and set this cost at approximately 20,800 $kcal/m^2$ per year for the summer–fall flora. Complete data were not available for the winter–spring flora, but a rough estimate suggests that stress values for that seasonal system are in the same order of magnitude.

Potential primary productivity of the winter–spring flora shown in Fig. 8.8 is based on greenhouse and growth-chamber gas-exchange measurements and on biomass determinations (Sharitz & McCormick, 1973). It appears that during the growing seasons of both of the above floras, potential plant productivity is similar. However, not all productivity is realized, due to environmental stressors. During each growing season, growth is explosive and conducive to rapid biomass accumulation and lowered respiration. Soon, however, moisture depletion, temperature change, and/or population interactions create conditions where growth becomes energetically too expensive to continue and respiration becomes greater than production. At the point where stress becomes maximum, dormancy is a distinctly advantageous condition *inter alia*, as it requires minimum energy for maintenance. Figure 8.2a supports field observations that dormancy begins in late May and early June for the spring flora and in September for the summer flora. During the following periods, most species are dormant and standing dead matter is at a maximum.

We conclude by emphasizing that, in granite-outcrop ecosystems, primary productivity of the system (which is potentially as high as that of many other ecosystems) is maximum when stress is at its minimum. Stored energy is utilized to maintain morphological adaptations to recurring environmental stresses.

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Summary

The influence of environmental stressors upon natural granite-outcrop ecosystems was described in terms of their structure and changes in ecosystem processes. The intensity of environmental stressors was quantified and found to correspond with soil depth. The intensity of stressors (moisture and temperature) increased with decreasing soil depth. Diurnal and seasonal patterns of stress occurred in these ecosystems. There was an inverse relationship between the intensity of stressors (described by a single index) and net biomass production. Species were distributed spatially and temporally in response to environmental stressors. Increasing stressor intensity resulted in decreasing species richness, changes in gas-exchange strategies of plants, lower structural complexity of the ecosystem, zonation of species, and in the seasonal alternation of two distinct floral assemblages. Total energy loss for the summer–fall flora was 20,800 kcal/m^2 per year. When stressors reach the maximum intensity, plants in the ecosystem enter a dormancy period. We concluded that the rate of primary productivity of granite-outcrop ecosystems is potentially as high as that of any other ecosystem measured. However, due to energy drains from environmental stressors, potential production is not attained. Productivity is high when stressors are at their minimum intensity. Stored energy is utilized to maintain morphological adaptations to recurring environmental stressors.

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